Beyond forest habitat qualities: climate and tree characteristics as the major drivers of epiphytic macrolichen assemblages in temperate mountains

P. Janssen, M. Fuhr, Christophe Bouget

To cite this version:

P. Janssen, M. Fuhr, Christophe Bouget. Beyond forest habitat qualities: climate and tree characteristics as the major drivers of epiphytic macrolichen assemblages in temperate mountains. Journal of Vegetation Science, 2019, 30 (1), pp.42-54. 10.1111/jvs.12701 . hal-02608954

HAL Id: hal-02608954

https://hal.inrae.fr/hal-02608954

Submitted on 30 Jun 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Beyond forest habitat qualities: climate and tree characteristics as the major drivers of epiphytic macrolichen assemblages in temperate mountains

Philippe Janssen[1], Marc Fuhr[1], Christophe Bouget[2]

[1] Université Grenoble-Alpes, National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), UR LESSEM, 2 rue de la Papeterie BP 76, F-38402 Saint-Martin-d'Hères, France

[2] National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), UR EFNO, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France

Correspondence

Philippe Janssen, Université Grenoble-Alpes, National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), UR LESSEM, 2 rue de la Papeterie BP 76, F-38402 Saint-Martin-d'Hères, France.

Email: philippe.janssen@irstea.fr

Running title: Habitat quality may not drive lichen diversity

Funding information

Financial support was provided by IRSTEA and local contributors (Conseil Général de l'Isère and Bauges Natural Regional Park).

ABSTRACT

Question

How are epiphytic macrolichen assemblages shaped by forest habitat quality as reflected by the availability of late-developmental forest attributes (i.e. stand maturity) and the temporal continuity of the wooded state (i.e. forest continuity)? Are these two forest habitat features the main drivers of lichen assemblages, and if so, at which spatial scale?

Location

Temperate mountain forests in the French Northern Alps.

Methods

In our sampling design, we defined treatments by crossing forest continuity (ancient vs recent) and stand maturity (mature vs overmature), then quantified lichen response to the treatments at the stand (n = 70) and tree scales (n = 420). We distinguished between total macrolichen and *Lobarion* species alone. Finally, we assessed the influence of tree-, stand- and landscape-scale variables, as well as climatic variables.

Results

Neither total macrolichen nor *Lobarion* diversity and composition were influenced by forest continuity, stand maturity or by stand- or landscape-associated variables. Instead, climatic variables, light availability at the stand scale and host tree characteristics were the major drivers of lichen assemblages. In our mountain forests, this clearly shows that macrolichen were more influenced by local abiotic and biotic factors than by present or past human-induced activities.

Conclusions

Overall, we show that assemblage patterns in forest ecosystems may be driven by parameters which are not directly related to habitat quality. The influences of forest continuity and stand maturity on diversity and composition thus appear to be context-dependent. In the ecological context of alpine forests, these findings highlight the benefits of selective-cutting practices and illustrate the importance of structural heterogeneity, in terms of both improved accessibility to light and tree

diameter diversity. Finally, the importance of temperature in shaping assemblage patterns suggests that global warming is probably the most significant threat to macrolichen conservation in temperate mountain forests.

Keywords: ancient forest, biodiversity conservation, epiphytic macrolichens, forest management, habitat quality, mountain forest, diversity patterns

INTRODUCTION

Biodiversity patterns are shaped by numerous environmental factors acting at multiple spatial scales (Levin 1992; Rosenzweig 1995). In forest ecosystems, species repartition may be influenced by climatic conditions at the large scale (Stevens 1989), by habitat amount and connectivity at the landscape scale (Fahrig 2013), by forest structure and composition at the stand scale (Barbier et al. 2008) and by deadwood or tree-related microhabitats at the tree scale (Müller et al. 2014). Overall it is now fairly well accepted that forest biodiversity is mostly influenced by two inherent and non-exclusive habitat qualities: stand maturity and forest continuity.

Stand maturity refers to a continuous process of tree and stand ageing, which depends on tree lifespan, the traditional harvest age of the dominant tree species and type of forest management. When comparing managed and unmanaged forests (e.g. Nascimbene et al. 2007; Nascimbene, Thor, et al. 2013) or young and old forests (e.g. Fenton & Bergeron 2008; Fritz, Niklasson, et al. 2008), numerous studies have pointed out the importance of stand maturity for forest biodiversity. Specifically, the availability of deadwood attributes or of very large trees has been shown to enhance the conservation of specialized species, such as some insects (e.g. Nilsson & Baranowski 1997), bryophytes (e.g. Spitale & Mair 2015) or birds (e.g. Bütler et al. 2004). This awareness has led to the development of silvicultural systems better able to increase, or at least maintain, stand maturity attributes and support multifunctional forests (Gustafsson et al. 2012).

Forest continuity refers to the maintenance of forest cover over time, regardless of stand maturity and management type. In Europe, forest continuity is closely related to the reforestation of previous agricultural areas since the mid-nineteenth century. We distinguish between ancient forests, which have existed continuously for centuries, and recent forests, which result from reforestation after a certain threshold date (Hermy & Verheyen 2007). Forest continuity has been shown to play a fundamental role in temperate forests for herbaceous plant assemblages (Hermy & Verheyen 2007), ectomycorrhizal fungi (Diedhiou et al. 2009), lichens and mosses (Fritz, Gustafsson, et al. 2008) and insects (Gossner et al. 2008). Two limitation processes have been highlighted: the poor dispersal ability of many ancient-forest species, impeding their colonization of recent forests (e.g. Verheyen et al. 2003); and recruitment limitations due to soil changes and competitive interactions (e.g. Honnay et al. 2002). Conservation strategies in several European countries now recommend primarily focusing on ancient forests (e.g. Fritz, Gustafsson, et al. 2008; Pătru-Stupariu et al. 2013).

Epiphytic lichens are among the most sensitive species groups known to respond to both stand maturity and forest continuity (Ellis 2012). Previous work has shown that epiphytic lichen diversity increases with stand maturity (Ranius et al. 2008; Moning et al. 2009; Nascimbene et al. 2009). Consequently, overmature stands are expected to host a larger epiphytic lichen diversity than mature stands (Nascimbene, Thor, et al. 2013). Also, few studies have pointed out the link between forest ancientness and epiphytic lichen assemblages (Rose 1976; Fritz, Gustafsson, et al. 2008; Marmor et al. 2011). Some lichen species have even been proposed as ancient forest indicators in England (Rose 1976) or in Sweden (Nitare & Norén 1992). Many of these indicator species have strict ecological requirements, such as the cyanolichens (Kuusinen 1996; Hedenås & Ericson 2008) or the *Lobarion pulmonariae* community (James et al. 1977; Ellis & Coppins 2007), and most of them are of conservation concern.

Although several studies have demonstrated the importance of overmature stands for lichen conservation, to the best of our knowledge, no studies have controlled for the potential cumulative effect of forest continuity. Moreover, in a recent review, Nascimbene et al. (2013) pointed out that the effect of forest continuity on lichen assemblage patterns has still rarely been explored despite the fact that this information is crucial to improving conservation-oriented management. Among epiphytic lichens, macrolichens (i.e. species with large thallus, restricted to fruticose, foliose and squamulose species in this study) and crustose lichens have both been shown to respond similarly to habitat alterations. Macrolichens, much easier to sample and to identify, could be good indicators of the conditions required by the entire lichen community (Bergamini et al. 2005). They are therefore often used as a proxy to assess the effect of forest management on total lichen diversity (e.g. Uliczka & Angelstam 1999; Nascimbene et al. 2009). At the same time, the *Lobarion* species belong to a community of epiphytic macrolichen sensitive to climate (i.e. cold-humid climate niche) and habitat quality (i.e. forest continuity) and are expected to be good indicators of old-growth forests (Kuusinen 1996; Hedenås & Ericson 2008).

Here, we tested whether the diversity and composition of total and *Lobarion* epiphytic macrolichen responded to forest continuity and stand maturity. As shifts in assemblage patterns are likely to result from a complex of different factors acting at different spatial scales (Jüriado et al. 2009; Király et al. 2013; Ódor et al. 2013), we also tested the relative influence of a set of tree-, stand- and landscape variables on epiphytic macrolichens, as well as climatic variables. Landscape variables were used to consider possible drivers underlying the effect of forest continuity, e.g. related to differences in the amount of favorable habitat in the surrounding landscapes at ancient and recent forest sites. Stand and tree variables were used to account for important local characteristics that may structure epiphytic macrolichen communities, beyond the influence of stand maturity and forest continuity. Based on this scheme, we addressed the following two questions: (i) Does forest continuity or stand maturity shape epiphytic macrolichen assemblages? (ii) Among tree, stand, landscape and climate factors, which have the greatest influence on epiphytic macrolichen assemblages?

MATERIALS and METHODS

Study area and experimental design

The study was carried out in the French pre-Alps in the Vercors, Chartreuse and Bauges ranges (Figure 1). These areas are characterized by a limestone substratum and a temperate climate. The landscapes are mostly covered by unfragmented forests and afforestation has mainly occurred above and below a persistent forest belt. Moreover, due to physical constraints and the lack of logging roads, the forests in our study have hitherto been less intensively managed than lowland forests (Paillet et al. 2015). Therefore, compared to recent lowland forests, recent mountain forests in the Northern Alps are mostly adjacent to ancient forests and have the potential to develop towards stand structures similar to those found in ancient forests.

In 2014, we sampled 70 sites located in mountain beech-fir forests at an altitude of 800 – 1500 m. The dominant tree species were European beech (*Fagus sylvatica*), Silver fir (*Abies alba*) and Norway spruce (*Picea abies*). Our stratified sampling design crossed forest continuity (ancient = 37; recent = 33) and stand maturity (mature = 33; overmature = 37), resulting in 22 ancient-mature sites, 15 ancient-overmature sites, 15 recent-mature sites and 18 recent-overmature sites. To insure independence among observations and avoid edge effects, all the sampling sites were established > 1 km away from any of the other sites, were located in ancient or recent forests > 5 ha in area, and were > 50 m from the nearest stand edge.

Forest continuity and stand maturity

Forest continuity was characterized by crossing digitized and georeferenced 1:40,000-scale État-Major maps of France, charted in the middle of the 19th century, with 1:10,000-scale current vegetation maps in a Geographic Information System managed with QGIS (QGIS Development Team 2015). Forest cover overlapping in both maps was considered to indicate ancient forests, while current forest cover overlapping with crops, pastures or meadows in the État-Major maps was considered to indicate recent forests. Around each of our selected ancient and recent forest sites (500 m radius), we controlled the État-Major maps using 1:5,000 or 1:2,500 cadastral plans drawn between 1730 and 1838. Finally, we used aerial photographs taken in the 1950s to confirm the continuity of the forest cover since the middle of the 19th century, at and around each site. Stand maturity was characterized on a 20-m-radius plot and a 10-m-radius subplot in which all standing trees and lying trunks were recorded (for further details, see Janssen et al. 2016). Mean canopy openness was estimated with a spherical densiometer from four points in the cardinal directions, 10 m away from the plot center. To distinguish between mature and overmature stands, we used hierarchical cluster analysis (Ward method) based on the first three axes of a principal component analysis (PCA) considering four environmental variables closely related to stand maturity: volume of large coarse woody debris (Ø > 30 cm), number of large snags (Ø > 30 cm), number of very large living trees (Ø > 62.5 cm), and tree microhabitat diversity (cumulative inertia of 88.30%).

Environmental variables

To model the response of epiphytic macrolichens to forest continuity and stand maturity, we used environmental variables in addition to continuity and maturity. Based on a recent review (Nascimbene et al., 2013), we selected nine a priori biologically important variables (Appendix S1 & Table 1). Climate variables – i.e. mean annual air temperature, total annual precipitation and mean relative air humidity – were derived from the SAFRAN climatic model (Durand et al. 1993) and adjusted for the effect of altitude following Kunstler et al. (2011). Landscape variables – i.e. distance to nearest forest edge, land-use diversity and forest proportion (within a 500-m radius) – were measured around each sampling site. Stand variables – i.e. mean canopy openness, total basal area and the number of very large trees – were extrapolated from the measurements taken within each 20-m-radius plot. Finally, the diameter and species (fir, spruce, beech or other deciduous trees) of the sampled trees were also considered.

Species inventory

Epiphytic macrolichens were surveyed in September, 2014, on the six largest live standing trees inside a 20-m-radius circular plot (mean (±SD) diameter of sampled trees for ancient-mature sites = 47.4 (±13.4) cm, ancient-overmature sites = 60.6 (±20.9) cm, recent-mature sites = 47.0 (±12.9) cm and recent-overmature sites = 54.8 (±20.1) cm). Samples for identification were collected mostly from European beech (n = 182) and silver fir (n = 160) at each plot, but when these two species were unavailable, Norway spruce (n = 50), Sycamore maple (*Acer pseudoplatanus*, n = 25), Common ash (*Fraxinus excelsior*, n = 2) or Mountain elm (*Ulmus glabra*, n = 1) were sampled. Based on this scheme, the cover percentage of each macrolichen species on each tree was visually estimated, from the base of the trunk up to a height of 2 m, using 5% cover classes. Moreover, because it has been shown that some groups of epiphytic lichens are more sensitive to stand maturity and forest continuity, we distinguished in subsequent analyses between total epiphytic macrolichen and *Lobarion pulmonariae* species, defined from James et al. (1977).

Statistical analysis

Analyses were performed with R version 3.3.2 (R Core Team 2017). Based upon data exploration, any independent variables with a skewness >1 were log or log+1 transformed to approximate normal distribution. For proportional data, logit transformation was applied. We then used two-way ANOVAs with type III sum of squares to test the significance of climate, landscape and stand variables to forest continuity, stand maturity and their interaction (Table 1).

To determine whether total and Lobarion epiphytic macrolichens richness and cover at the plot scale (n = 70) were influenced by forest continuity, stand maturity or their interaction, we used two-way ANOVAs. We then investigated whether diversity patterns were predicted by climate, stand or landscape variables, using 48 a priori candidate linear models, plus the null model (Appendix S2). Because richness and cover may not be independent, we also assessed model performance with standardized richness by including "Cover" as a covariate. Also, because significant differences in total richness and cover between the three mountain ranges were identified, we added "latitude" as a covariate in all the candidate models. We then fit Poisson linear models for richness and negative binomial linear models for cover and controlled for multicolinearity among explanatory variables with variance inflation factors. The variance explained by the GLMs was estimated with the adjusted coefficient of determination; the most parsimonious regression model was identified with the Akaike information criterion corrected for small sample sizes (AICc); and we used model averaging to estimate parameter and associated unconditional standard errors based on the subset of top ranking models for which the sum of AICc weights reached ≥0.95 (Burnham & Anderson 2002). To determine whether the inclusion of tree characteristics improved the models' predictive power, we used General Linear Mixed Models (GLMMs). Total and Lobarion epiphytic macrolichens richness and cover at each tree (n = 420) were used as dependent variables, as well as the standardized richness. We then investigated whether diversity patterns were predicted by tree species and diameter variables, as well as the most influential environmental variables at the plot scale (i.e. temperature and mean canopy openness), using 12 a priori candidate linear models, plus the null model (Appendix S3). For *Lobarion* species, observed on deciduous trees only (European beech, n = 28; other deciduous trees, n = 7), we tested all possible combinations of models formed by tree diameter and the most influential environmental variables at the plot scale (n models = 5). We then fit Poisson linear mixed models for richness and negative binomial linear mixed models for cover with "plot" as a random effect and "latitude" as a covariate in all the candidate models. We used the marginal coefficient of determination for fixed effect parameters alone to estimate the variance explained by the GLMMs (Nakagawa et al. 2017). We then ranked the models according to their AICc values and used model averaging to estimate the parameters.

To determine whether epiphytic macrolichen composition was influenced by forest continuity, stand maturity or their interaction, we performed PERMANOVA (i.e. between-groups) and PERMDISP (i.e. within-group) analyses (Anderson & Walsh 2013) based on a Bray-Curtis distance, with 999 permutations. We then used canonical analysis of principal coordinates (CAP, Anderson & Willis 2003) based on a Bray-Curtis distance matrix, with 999 permutations, at the plot scale, to determine whether climate, stand or landscape variables explain epiphytic macrolichen assemblage variations; at the tree scale, to determine whether the inclusion of tree characteristics allows for a better understanding of epiphytic macrolichens assemblage variations (after removing trees for which no macrolichen species were recorded (n = 103)). At the plot and tree scales, we calculated the marginal contribution of all independent variables to total constrained inertia and tested for their individual significance (after all other variables were partialled out). Finally, composition analyses of Lobarion species were not performed because they were rarely observed at the plot (n = 23) and tree (n = 35) scales.

RESULTS

Variations in environmental variables in relation to forest continuity and stand maturity

Stand and landscape variables varied according to forest continuity and stand maturity classification (Table 1). Indeed, mean canopy openness, stem basal area and the number of very large trees increased from mature to overmature stands. Compared to recent forest sites, ancient forest sites were included in a less diversified matrix, that contained more forests overall, and were located at a greater distance from the forest edge. Climate variables, on the other hand, were not clearly related to forest continuity or to stand maturity. Only total annual precipitation increased from ancient to recent forest sites, even though the effect size was low.

The interaction term between forest continuity and stand maturity was non-significant for almost all the tested variables (Table 1), indicating that variations were consistent between ancient and recent forests, at a comparable level of maturity.

Diversity patterns for epiphytic macrolichens at the stand and tree scales

Overall, 33 species of epiphytic macrolichens were recorded at the 70 sites (Appendix S4), including 10 *Lobarion* species. Total and *Lobarion* species richness ranged from 1-16 species and from 0-4 species, and averaged six species (SD ±3.55) and 0.5 species (SD ±0.91) per site, respectively.

At the stand scale, two-way ANOVAs revealed no difference in total or *Lobarion* richness or cover between ancient and recent forests, mature and overmature stands or between ancient-mature, ancient-overmature, recent-mature and recent-overmature stands (Appendix S5). GLMs results showed that total richness and cover, as well as standardized total richness, were best predicted by the same model, which accounted for temperature and mean canopy openness (Table 2). For

Lobarion species, GLMs results showed that richness was best predicted by a model accounting for basal area and forest proportion in the surrounding landscape, that cover was best predicted by the null model and that standardized richness was best predicted by a model accounting for cover only. Except for total richness (AICc weights = 0.984), model selection uncertainty still remained for all the dependent variables. Model averaging revealed that total richness and cover, as well as standardized richness, increased with decreasing temperatures and with increasing mean canopy openness (Table 3). For Lobarion species, richness increased with stand basal area. However, for both Lobarion richness and cover, the null model was among the top-ranking models.

At the tree scale, GLMMs results showed that total richness and cover were best predicted by the same model, which accounted for temperature, mean canopy openness and tree species, while standardized total richness was best predicted by a model accounting for lichen cover, temperature and tree species (Table 4). For Lobarion species, GLMMs results showed that richness and cover were both best predicted by the same model, which accounted for mean canopy openness and tree diameter, while standardized Lobarion richness was best predicted by a model accounting for lichen cover, mean canopy openness and tree diameter (Table 4). However, model selection uncertainty still remained for all the dependent variables. Model averaging revealed that total richness and cover increased with mean canopy openness but that total richness and cover, as well as standardized total richness, decreased with increasing temperature (Table 5). Moreover, with Silver fir as a reference, total richness and cover, as well as standardized richness, decreased on European beech and other deciduous trees, while cover only decreased on Norway spruce. For Lobarion species, richness and cover, as well as standardized richness, increased with tree diameter, while standardized richness only increased with mean canopy openness (Table 5).

Variations in epiphytic macrolichen composition at stand and tree scales

Lichens composition was influenced neither by forest continuity (PERMANOVA pseudo-$F_{1,68}$ = 0.661, p = 0.706), nor by stand maturity (PERMANOVA pseudo-$F_{1,68}$ = 1.712, p = 0.116) or maturity-continuity interaction (PERMANOVA pseudo-$F_{1,68}$ = 0.606, p = 0.762). Moreover, PERMDISP revealed no significant differences in the average within-group distances, thus supporting the absence of variation in assemblage structure among treatments.

At the stand scale, CAP ordination revealed that 22.5% ($p = 0.001$) of the variation in species composition was explained by environmental variables (Figure 2 & Appendix S6 for elementary contributions of variables to inertia). The first CAP axis was positively related to latitude (12.9%, $p = 0.001$) and temperature (17.6%, $p = 0.001$) but negatively related to canopy openness (15.2%, $p = 0.005$). The second CAP axis was positively related to precipitation (14.4%, $p = 0.043$). All the other variables did not significantly influence species composition. At the tree scale, CAP ordination revealed that 15.1% ($p = 0.001$) of the variation in species composition was explained by tree characteristics and environmental variables (Figure 2 & Appendix S7). The first CAP axis was positively related to latitude (8.3%, $p = 0.001$) and temperature (14.1%, $p = 0.001$). The second CAP axis was positively related to canopy openness (14.5%, $p = 0.001$) and negatively related to tree diameter (3.6%, $p = 0.001$). Also, tree species explained a large part of the variation in species composition (31.1%, $p = 0.001$), with a clear pattern opposing deciduous from coniferous trees along the two CAP axes.

DISCUSSION

In unfragmented mountain forests, our results clearly show that climate parameters, light availability at the stand scale and host-tree characteristics were the major drivers of epiphytic macrolichen diversity and composition. Neither forest habitat qualities, i.e. maturity and continuity factors, nor stand- and landscape-associated variables, affected by present and past human activities, were of any inferential value.

Forest continuity and stand maturity are not the main drivers of epiphytic macrolichen assemblages

Contrary to our expectations, the assemblage patterns of epiphytic macrolichens were not influenced by forest continuity and landscape-associated variables. This surprising lack of a legacy effect is interesting given the large number of studies that have demonstrated the influence of forest continuity on biodiversity (Hermy & Verheyen 2007). Previous studies have, indeed, reported a significant effect of forest continuity on lichens (Fritz, Gustafsson, et al. 2008; Moning et al. 2009; Marmor et al. 2011), especially on the most demanding species, such as the *Lobarion* macrolichens and the cyanolichens (Rose 1976; Kuusinen 1996; Ellis & Coppins 2007). Nonetheless, studies conducted in forest-dominated landscapes with good habitat connectivity, as was the case in the Northern Alps, only found a limited effect of forest continuity and landscape factors on lichen assemblages (Dittrich et al. 2013; Király et al. 2013; Ódor et al. 2013). . Fragmentation worsens dispersal limitations (Jamoneau et al. 2012), and since colonization efficiency depends on habitat availability at the landscape scale (De Frenne et al. 2011), the lichen species in our study area appear to have been able to rapidly colonize recent forests. Moreover, as elsewhere in European mountain areas (e.g. Gellrich et al. 2007), reforestation has largely occurred next to ancient forests, thus reducing the distance to habitat source and limiting dispersal barriers within the habitat matrix (Honnay et al. 2002). For all these reasons, we infer that the distance between regeneration units and potential sources of propagules in the Northern Alps is sufficiently low to not limit epiphytic macrolichen dispersal and establishment in recent forests (e.g. Hilmo 2002; Werth et al. 2006). However, even in this unfragmented forest landscape, forest continuity and landscape variables cannot be ruled out as influencing factors, particularly for dispersal-limited epiphytic species with strong substrate-specific requirements such as certain crustose and leprose lichen species (e.g. Marmor et al. 2011; Kubiak & Osyczka 2017).

In addition, assemblage patterns were not influenced by stand maturity and stand-associated variables. These results contrast with current knowledge on the importance of old-growth forest attributes for biodiversity. Indeed, numerous studies have pointed out a direct link between the availability of larger, older trees at the stand scale and lichen diversity (Kuusinen 1996; Fritz, Niklasson, et al. 2008; Ranius et al. 2008; Marmor et al. 2011). In our study area, the availability of large standing trees did not structure diversity and composition, even though we inventoried five times as many such trees in overmature than mature stands. This lack of any stand-maturity influence on epiphytic macrolichens may be due to the relatively high habitat quality of both the mature and overmature stands in the Alps resulting from selective-cutting management practices (Nascimbene et al. 2007; Dymytrova et al. 2014). Combined with landscape homogeneity, this may have facilitated species dispersion and establishment on a large number of host trees (Ellis 2012; Nascimbene, Thor, et al. 2013). Moreover, as in the Italian Alps (Nascimbene, Dainese, et al. 2013), we found that light conditions was one of the most powerful predictor of total epiphytic macrolichen diversity and composition at the stand scale. Indeed, it is well known that lichen species avoid shady conditions and that these photosynthetic organisms benefit from an increase in canopy openness (Uliczka & Angelstam 1999; Moning et al. 2009; Jüriado et al. 2009; Ódor et al. 2013). Overall, since availability and heterogeneity of light are expected to increase during forest succession in adult stands due to changes in the canopy - gap structure, our results confirm the positive effect of management practices aiming at maintaining or enhancing stand structural heterogeneity (Ellis 2012; Nascimbene, Thor, et al. 2013), such as selective cutting and retention forestry (Gustafsson et al. 2012).

Climate and tree species characteristics better explain epiphytic macrolichen assemblages

Among all of the environmental variables we tested, temperature best explained epiphytic macrolichen assemblages at the stand scale, with higher temperatures producing an overall negative effect on diversity. This result is quite surprising given that, in our sampling design, we controlled for differences in altitude among treatments. The effect of temperature was thus more likely due to small intra-group variations (i.e. standard deviation in altitude = ±140 m) than to broad altitudinal gradients. Indeed, in mountain areas, altitude and exposure exacerbate climatic differences, and substantial changes can be found over small distances. Climate is known to greatly influence lichen species distribution at large scale (Werth et al. 2005; Ellis & Coppins 2007). At a smaller scale, however, it has been suggested that stand structure parameters would better explain lichen diversity patterns than would climatic parameters (Moning et al. 2009). Controlling for differences in forest structure, Bässler et al. (2016) recently showed that lichen diversity increased with decreasing temperatures in Bohemian mountain forests, and that this increase was above all driven by an increase in the number of foliose and fruticose species. These findings corroborate previous ones in the Alps (Nascimbene & Marini 2015) and Carpathian Mountains (Dymytrova et al. 2014), and give weight to the view that macrolichen diversity peaks at mid elevations (Rapai et al. 2012). We believe that the strong effect of temperature we found in the Northern Alps is related to optimal performances of the mountain beech-fir macrolichen community in colder climates. This view is supported by the fact that we recorded numerous species (e.g. *Hypogymnia physodes*, *Parmelia saxatilis*, *Parmeliopsis ambigua*) characteristic of a cold-humid climate niche (Giordani & Incerti 2008). However, contrary to numerous other studies (e.g. Giordani & Incerti 2008; Marini et al. 2011; Coyle & Hurlbert 2016), we found no strong relationship between atmospheric water supply and epiphytic macrolichen assemblages. This may be due to the substantial yearly amounts of rainfall occurring in the three studied mountain ranges (mean annual precipitation >1500 mm).

Tree characteristics greatly influenced assemblages of epiphytic macrolichens. Especially, total species richness and cover were higher on silver fir than on other tree species, while *Lobarion* species were exclusively found on deciduous trees. Tree species identity is a well-known driver of epiphytic lichen composition and numerous studies have also reported a significant effect on species diversity (Moning et al. 2009; Király et al. 2013; Ódor et al. 2013). Specifically, in mountain beech-fir forests, it has been shown that the two dominant tree species hosted different communities, thus increasing lichen richness at the stand scale (Nascimbene et al. 2009). Host-use preferences is closely related to differences in the physical and chemical properties of the bark substratum (Ellis 2012; Nascimbene, Thor, et al. 2013). Our findings support the common suggestion that conservation-oriented forest management should maintain tree species diversity (Ellis 2012; Nascimbene, Thor, et al. 2013; Ódor et al. 2013). However, in our study, the greater species richness we found on silver fir was more probably linked to a sampling bias, since the sampled fir trees had a larger diameter than the other sampled species (Silver fir, DBH = 68 cm ± 15; Norway spruce, DBH = 58 cm ± 11; European beech, DBH = 43 cm ± 15; other deciduous trees, DBH = 41 cm ± 10). Indeed, high epiphytic lichen diversity is often reported on larger trees (Moning et al. 2009; Jüriado et al. 2009), in line with our results on *Lobarion* diversity and composition. Epiphytic macrolichen conservation, particularly for *Lobarion* species, would benefit from the maintenance of very large trees, especially deciduous trees.

Conclusion

The effects of forest continuity and stand maturity on lichen assemblages are supposedly context-dependent. Within our relatively homogeneous mountain forests, neither epiphytic macrolichen diversity nor composition responded to stand maturity and forest continuity. Using lichen species as indicators of ancient forests must therefore be cautious (Nordén & Appelqvist 2001; Fenton & Bergeron 2008). Our results point out the importance of structural heterogeneity at the stand and tree scales in improving both light and tree-diameter diversity. In mixed mountain forests, selection cutting which maintains an uneven-aged structure with trees of all sizes and species should therefore be promoted. These management practices make it possible to balance wood production and biodiversity conservation, even for the demanding *Lobarion* macrolichens. Finally, we found an important negative effect of rising temperatures on assemblage patterns suggesting that global warming is probably the most significant threat for macrolichen conservation in temperate mountain forests (e.g. Nascimbene et al. 2016). Overall then, assemblage patterns are not regulated by single-scale environmental parameters but by processes acting at both regional and local scales (Coyle & Hurlbert 2016). Conservation strategies should therefore be systematically based on a multiple-scale environmental evaluation.

DATA ACCESSIBILITY STATEMENT

The research data supporting this publication are provided in Supplementary Material (Online Publication Only).

ACKNOWLEDGEMENTS

We thank Gilles Favier, Sophie Labonne, Fanny Lebagousse and Pascal Tardif from IRSTEA for help in the field. We also thank Vicki Moore for correcting the English manuscript.

REFERENCES

Anderson, M.J., & Walsh, D.C. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83: 557–574.

Anderson, M.J., & Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84: 511–525.

Barbier, S., Gosselin, F., & Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. *Forest Ecology and Management* 254: 1–15.

Bässler, C., Cadotte, M.W., Beudert, B., Heibl, C., Blaschke, M., Bradtka, J.H., Langbehn, T., Werth, S., & Müller, J. 2016. Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography* 39: 689–698.

Bergamini, A., Scheidegger, C., Stofer, S., Carvalho, P., Davey, S., Dietrich, M., Dubs, F., Farkas, E., Groner, U., Kärkkäinen, K., Keller, C., Lökös, L., Lommi, S., Máguas, C., Mitchell, R., Pinho, P., Rico, V.J., Aragón, G., Truscott, A.-M., Wolseley, P., & Watt, A. 2005. Performance of macrolichens and lichen genera as indicators of lichen species richness and composition. *Conservation Biology* 19: 1051–1062.

Burnham, K.P., & Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed.* Springer-Verlag, New York.

Bütler, R., Angelstam, P., Ekelund, P., & Schlaepfer, R. 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biological Conservation* 119: 305–318.

Coyle, J.R., & Hurlbert, A.H. 2016. Environmental optimality, not heterogeneity, drives regional and local species richness in lichen epiphytes. *Global Ecology and Biogeography* 25: 406–417.

De Frenne, P., Baeten, L., Graae, B.J., Brunet, J., Wulf, M., Orczewska, A., Kolb, A., Jansen, I., Jamoneau, A., Jacquemyn, H., Hermy, M., Diekmann, M., De Schrijver, A., De Sanctis, M., Decocq, G., Cousins, S.A.O., & Verheyen, K. 2011. Interregional variation in the floristic recovery of post-agricultural forests: Recovery of post-agricultural forest. *Journal of Ecology* 99: 600–609.

Diedhiou, A.G., Dupouey, J.-L., Buée, M., Dambrine, E., Laüt, L., & Garbaye, J. 2009. Response of ectomycorrhizal communities to past Roman occupation in an oak forest. *Soil Biology & Biochemistry* 41: 2206–2213.

Dittrich, S., Hauck, M., Schweigatz, D., Dörfler, I., Hühne, R., Bade, C., Jacob, M., & Leuschner, C. 2013. Separating forest continuity from tree age effects on plant diversity in the ground and epiphyte vegetation of a Central European mountain spruce forest. *Flora* 208: 238–246.

Durand, Y., Brun, E., Mérindol, L., Guyomarc'h, G., Lesaffre, B., & Martin, E. 1993. A meteorological estimation of relevant parameters for snow models. *Annals of Glaciology* 18: 65–71.

Dymytrova, L., Nadyeina, O., Hobi, M.L., & Scheidegger, C. 2014. Topographic and forest-stand variables determining epiphytic lichen diversity in the primeval beech forest in the Ukrainian Carpathians. *Biodiversity and Conservation* 23: 1367–1394.

Ellis, C.J. 2012. Lichen epiphyte diversity: A species, community and trait-based review. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 131–152.

Ellis, C.J., & Coppins, B.J. 2007. Changing climate and historic-woodland structure interact to control species diversity of the 'Lobarion'epiphyte community in Scotland. *Journal of Vegetation Science* 18: 725–734.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis (K. Triantis, Ed.). *Journal of Biogeography* 40: 1649–1663.

Fenton, N.J., & Bergeron, Y. 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. *Biological Conservation* 141: 1389–1399.

Fritz, Ö., Gustafsson, L., & Larsson, K. 2008. Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation* 141: 655–668.

Fritz, Ö., Niklasson, M., & Churski, M. 2008. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science* 12: 93–106.

Gellrich, M., Baur, P., Koch, B., & Zimmermann, N.E. 2007. Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. *Agriculture, Ecosystems & Environment* 118: 93–108.

Giordani, P., & Incerti, G. 2008. The influence of climate on the distribution of lichens: a case study in a borderline area (Liguria, NW Italy). *Plant Ecology* 195: 257–272.

Gossner, M.M., Engel, K., & Jessel, B. 2008. Plant and arthropod communities in young oak stands: are they determined by site history? *Biodiversity and Conservation* 17: 3165–3180.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., & Franklin, J.F. 2012. Retention Forestry to Maintain Multifunctional Forests: A World Perspective. *BioScience* 62: 633–645.

Hedenås, H., & Ericson, L. 2008. Species occurrences at stand level cannot be understood without considering the landscape context: Cyanolichens on aspen in boreal Sweden. *Biological Conservation* 141: 710–718.

Hermy, M., & Verheyen, K. 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research* 22: 361–371.

Hilmo, O. 2002. Growth and morphological response of old-forest lichens transplanted into a young and an old Picea abies forest. *Ecography* 25: 329–335.

Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H., & Hermy, M. 2002. Ecological perspectives for the restoration of plant communities in European temperate forests. *Biodiversity & Conservation* 11: 213–242.

James, P.W., Hawksworth, D.L., & Rose, F. 1977. Lichen communities in the British Isles: a preliminary conspectus. In Seaward, M.R.D. (ed.), *Lichen Ecology*, pp. 295–413. Academic press, London.

Jamoneau, A., Chabrerie, O., Closset-Kopp, D., & Decocq, G. 2012. Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography* 35: 124–133.

Janssen, P., Cateau, E., Fuhr, M., Nusillard, B., Brustel, H., & Bouget, C. 2016. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodiversity and Conservation* 25: 1167–1185.

Jüriado, I., Liira, J., Paal, J., & Suija, A. 2009. Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. *Biodiversity and Conservation* 18: 105–125.

Király, I., Nascimbene, J., Tinya, F., & Ódor, P. 2013. Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiversity and Conservation* 22: 209–223.

Kubiak, D., & Osyczka, P. 2017. Specific Vicariance of Two Primeval Lowland Forest Lichen Indicators. *Environmental Management* 59: 966–981.

Kunstler, G., Albert, C.H., Courbaud, B., Lavergne, S., Thuiller, W., Vieilledent, G., Zimmermann, N.E., & Coomes, D.A. 2011. Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *Journal of Ecology* 99: 300–312.

Kuusinen, M. 1996. Cyanobacterial macrolichens on Populus tremula as indicator of forest continuity in Finland. *Biological Conservation* 75: 43–49.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Marini, L., Nascimbene, J., & Nimis, P.L. 2011. Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure. *Science of The Total Environment* 409: 4381–4386.

Marmor, L., Tõrra, T., Saag, L., & Randlanea, T. 2011. Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. *Ecological Indicators* 11: 1270–1276.

Moning, C., Werth, S., Dziock, F., Bässler, C., Bradtka, J., Hothorn, T., & Müller, J. 2009. Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management* 258: 745–751.

Müller, J., Jarzabek-Müller, A., Bussler, H., & Gossner, M.M. 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation* 17: 154–162.

Nakagawa, S., Johnson, P.C.D., & Schielzeth, H. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface* 14: 20170213.

Nascimbene, J., Casazza, G., Benesperi, R., Catalano, I., Cataldo, D., Grillo, M., Isocrono, D., Matteucci, E., Ongaro, S., Potenza, G., Puntillo, D., Ravera, S., Zedda, L., & Giordani, P. 2016. Climate change fosters the decline of epiphytic Lobaria species in Italy. *Biological Conservation* 201: 377–384.

Nascimbene, J., Dainese, M., & Sitzia, T. 2013. Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. *Forest Ecology and Management* 289: 325–332.

Nascimbene, J., & Marini, L. 2015. Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. *Journal of Biogeography* 42: 1222–1232.

Nascimbene, J., Marini, L., & Nimis, P.L. 2007. Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. *Forest Ecology and Management* 247: 43–47.

Nascimbene, J., Marini, L., & Nimis, P.L. 2009. Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. *Canadian Journal of Forest Research* 39: 785–791.

Nascimbene, J., Thor, G., & Nimis, P.L. 2013. Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe – A review. *Forest Ecology and Management* 298: 27–38.

Nilsson, S.G., & Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* 20: 491–498.

Nitare, J., & Norén, M. 1992. Nyckelbiotoper kartläggs i nytt projekt vid Skogsstyrelsen. *Svensk Botanisk Tidskrift* 86: 219–223.

Nordén, B., & Appelqvist, T. 2001. Conceptual problems of Ecological Continuity and its bioindicators. *Biodiversity and Conservation* 10: 779–791.

Ódor, P., Király, I., Tinya, F., Bortignon, F., & Nascimbene, J. 2013. Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *Forest Ecology and Management* 306: 256–265.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., & Gosselin, F. 2015. Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management* 346: 51–64.

Pătru-Stupariu, I., Angelstam, P., Elbakidze, M., Huzui, A., & Andersson, K. 2013. Using forest history and spatial patterns to identify potential high conservation value forests in Romania. *Biodiversity and Conservation* 22: 2023–2039.

QGIS Development Team. 2015. *QGIS Geographic Information System. Open Source Geospatial Foundation Project.*

R Core Team. 2017. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Ranius, T., Johansson, P., Berg, N., & Niklasson, M. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of Vegetation Science* 19: 653–662.

Rapai, S.B., McMullin, R.T., & Newmaster, S.G. 2012. The importance of macrolichen traits and phylogeny in forest community assemblage along a high elevation gradient in southwestern British Columbia. *Forest Ecology and Management* 274: 231–240.

Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. In *Lichenology: Progress and Problems*, pp. 278–307. Brown, D.H., Hawksworth, D.L. & Bailey, R.H., London.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Spitale, D., & Mair, P. 2015. Predicting the distribution of a rare species of moss: The case of Buxbaumia viridis (Bryopsida, Buxbaumiaceae). *Plant Biosystems* In press:

Stevens, G.C. 1989. The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in theTropics. *The American Naturalist* 133: 240–256.

Uliczka, H., & Angelstam, P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* 22: 396–405.

Verheyen, K., Guntenspergen, G.R., Biesbrouck, B., & Hermy, M. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *Journal of Ecology* 91: 731–742.

Werth, S., Tømmervik, H., & Elvebakk, A. 2005. Epiphytic macrolichen communities along regional gradients in northern Norway. *Journal of Vegetation Science* 16: 199–208.

Werth, S., Wagner, H.H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J.M., & Scheidegger, C. 2006. Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology* 87: 2037–2046.

SUPPORTING INFORMATION

Appendix S1. Correlation matrix of environmental variables used to model macrolichen assemblages.

Appendix S2. Candidate models used to model macrolichen diversity at the stand scale.

Appendix S3. Candidate models used model macrolichen diversity at the tree scale.

Appendix S4. List of epiphytic macrolichen species recorded in the Northern Alps.

Appendix S5. Variations in macrolichen diversity in relation to forest continuity and stand maturity factors.

Appendix S6. Elementary contributions of environmental variables to inertia in the CAP of macrolichens communities.

Appendix S7. Elementary contributions of tree characteristics and environmental variables to inertia in the CAP of macrolichens communities.

Appendix S8. Raw data at the stand scale.

Appendix S9. Raw data at the tree scale.

Appendix S10. Site by species matrix of epiphytic macrolichens at the stand scale.

Appendix S11. Site by species matrix of epiphytic macrolichens at the tree scale.

Table 1. Variations in site, climate, stand and landscape variables between ancient-mature sites (Anc-Mat), ancient-overmature sites (Anc-Ove), recent-mature sites (Rec-Mat) and recent-overmature sites (Rec_Ove) in the French Northern Alps (DBH = diameter at breast height). Two-way ANOVAs test the significance of environmental variables to forest continuity (FC), stand maturity (SM) and their interaction (INTER).

Variables	Description	Anc-Mat Mean (±SD)	Anc-Ove Mean (±SD)	Rec-Mat Mean (±SD)	Rec-Ove Mean (±SD)	FC p-value	SM p-value	INTER p-value
Site variables								
Lati	Latitude (decimal degrees)	45.33 (±0.23)	45.50 (±0.23)	45.44 (±0.23)	45.50 (±0.22)	0.164	0.035	0.340
Long	Longitude (decimal degrees)	5.78 (±0.26)	5.94 (±0.25)	5.91 (±0.25)	5.94 (±0.27)	0.135	0.081	0.304
Alti	Altitude (meters)	1179 (±129)	1145 (±145)	1073 (±133)	1102 (±144)	0.024	0.457	0.348
Slope	Slope (%)	23.56 (±6.56)	24.98 (±8.38)	25.63 (±8.14)	25.61 (±7.08)	0.410	0.571	0.691
Expo	Exposure (degrees)	231.8 (±96.8)	232.7 (±115.2)	217.6 (±114.8)	246.3 (±112.3)	0.698	0.981	0.599
Climate variables								
Temp	Mean annual temperature (°C)	6.73 (±0.58)	6.90 (±0.78)	7.14 (±0.60)	7.05 (±0.70)	0.069	0.444	0.426
Precip	Sum annual precipitation (mm)	1579 (±272)	1687 (±151)	1746 (±198)	1628 (±218)	0.027	0.150	0.038
Humi	Mean relative humidity (g/kg)	5.67 (±0.30)	5.70 (±0.24)	5.60 (±0.22)	5.74 (±0.31)	0.486	0.745	0.440
Stand variables								

Canop	Mean canopy openness (%)	8.39 (±3.44)	13.52 (±6.01)	9.02 (±4.41)	11.31 (±6.14)	0.743	0.006	0.267
Basal_area	Total stems basal area (m^2)	5.65 (±1.59)	6.68 (±1.89)	6.26 (±1.93)	7.96 (±1.73)	0.270	0.045	0.489
Large_trees	Number of very large trees (DBH > 62.5 cm)	0.77 (±1.07)	5.93 (±3.83)	0.73 (±0.59)	5.83 (±2.77)	0.693	0.000	0.971
Landscape variables (500-m-radius)								
Alpha_LU	Land-use diversity	2.59 (±1.14)	2.40 (±0.91)	3.33 (±0.90)	2.78 (±1.00)	0.000	0.429	0.528
Dist_Forest	Distance to the nearest forest edge (meters)	557 (±489)	554 (±373)	230 (±131)	468 (±313)	0.002	0.588	0.107
Prop_Forest	Forest proportion (%)	90.79 (±11.74)	94.56 (±9.22)	79.72 (±14.79)	93.06 (±8.20)	0.006	0.364	0.119

Table 2. Top-ranking models among 49 a priori models predicting diversity patterns of total and *Lobarion* epiphytic macrolichens at the stand scale in the French Northern Alps, as assessed with Akaike's information criterion corrected for small sample size (AICc). Number of estimated parameters including the intercept (k), AICc, , AICc weight (*W*), adjusted coefficient of determination (R^2_{adj}) and evidence ratio (ER), i.e. Akaike weight of the best model/Akaike weight of the second best model, are provided.

Dependent variable	Model	k	AICc	*W*	R^2_{adj}	ER
Total richness	Canop + Temp	4	332.8	0.984	0.591	328.00
Total cover	Canop + Temp	5	663.3	0.427	0.421	2.98
Standardized total richness	Cover + Canop + Temp	5	304.8	0.356	0.736	2.25
Lobarion richness	Basal_area + Prop_Forest	4	140.0	0.127	0.151	1.03
Lobarion cover	Null	2	213.6	0.161	0.000	2.77
Standardized Lobarion richness	Cover	2	84.9	0.261	0.667	5.22

Table 3. Relative importance (Imp.), average coefficients (Estimate (±SE)) and confidence intervals (95% CI) for each variable predicting total and *Lobarion* epiphytic macrolichen richness and cover at the stand scale in the French Northern Alps. The 95% confidence interval of coefficients shaded excluded 0.

Parameter	Total richness			Total cover			Standardized total richness		
	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)
Cover	NA	NA	NA	NA	NA	NA	1.00	0.005 (±0.001)	(0.003; 0.007)
Lati	1	-0.737 (±0.222)	(-1.172; -0.302)	1.00	-1.424 (±0.455)	(-2.315; -0.533)	1.00	-0.183 (±0.252)	(-0.677; 0.311)
Temp	1	-0.343 (±0.083)	(-0.506; -0.180)	0.92	-0.489 (±0.149)	(-0.781; -0.198)	0.99	-0.273 (±0.087)	(-0.444; -0.103)
Precip	NA	NA	NA	0.28	-0.001 (±0.001)	(-0.002; 0.000)	0.07	0.000 (±0.000)	(-0.001; 0.001)
Humi	NA	NA	NA	0.17	-3.405 (±2.583)	(-8.467; 1.658)	0.08	0.765 (±1.198)	(-1.583; 3.113)
Canop	1	0.353 (±0.091)	(0.175; 0.531)	0.52	0.447 (±0.174)	(0.106; 0.788)	0.38	0.193 (±0.098)	(0.000; 0.386)
Basal_area	NA	NA	NA	0.06	-0.323 (±0.337)	(-0.984; 0.338)	0.06	0.116 (±0.180)	(-0.237; 0.469)
Large_Tree	NA	NA	NA	0.08	-0.163 (±0.117)	(-0.394; 0.067)	0.05	0.005 (±0.061)	(-0.114; 0.124)
Alpha_LU	NA	NA	NA	0.02	-0.047 (±0.091)	(-0.225; 0.131)	0.06	-0.027 (±0.053)	(-0.132; 0.078)
Dist_Forest	NA	NA	NA	0.02	-0.030 (±0.120)	(-0.266; 0.206)	0.06	0.032 (±0.069)	(-0.103; 0.166)
Prop_Forest	NA	NA	NA	0.02	0.031 (±0.079)	(-0.123; 0.185)	0.09	0.047 (±0.046)	(-0.044; 0.137)

Parameter	*Lobarion* richness			*Lobarion* cover			Standardized *Lobarion* richness		
	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)
Cover	NA	NA	NA	NA	NA	NA	1.00	0.332 (±0.046)	(0.243; 0.421)
Lati	0.97	-0.556 (±0.783)	(-2.091; 0.979)	0.83	0.243 (±1.409)	(-2.518; 3.004)	0.73	0.080 (±0.720)	(-1.331; 1.491)
Temp	0.06	0.127 (±0.276)	(-0.414; 0.668)	0.11	0.238 (±0.508)	(-0.758; 1.234)	0.12	-0.143 (±0.314)	(-0.758; 0.472)
Precip	0.14	-0.001 (±0.001)	(-0.003; 0.001)	0.20	-0.002 (±0.002)	(-0.006; 0.001)	0.09	0.000 (±0.001)	(-0.002; 0.003)
Humi	0.06	-1.915 (±4.603)	(-10.937; 7.108)	0.12	-6.583 (±8.437)	(-23.120; 9.953)	0.13	2.593 (±4.353)	(-5.939; 11.125)
Canop	0.25	0.481 (±0.315)	(-0.136; 1.099)	0.28	0.900 (±0.531)	(-0.141; 1.942)	0.12	0.118 (±0.368)	(-0.604; 0.839)
Basal_area	0.79	1.576 (±0.622)	(0.357; 2.795)	0.18	0.957 (±1.073)	(-1.146; 3.059)	0.11	-0.113 (±0.556)	(-1.202; 0.977)
Large_Tree	0.20	0.282 (±0.258)	(-0.225; 0.788)	0.10	0.196 (±0.370)	(-0.529; 0.922)	0.09	0.003 (±0.217)	(-0.423; 0.429)
Alpha_LU	0.05	-0.029 (±0.186)	(-0.393; 0.335)	0.09	0.084 (±0.328)	(-0.558; 0.727)	0.17	-0.150 (±0.206)	(-0.554; 0.253)
Dist_Forest	0.12	0.270 (±0.227)	(-0.174; 0.714)	0.17	0.466 (±0.447)	(-0.410; 1.341)	0.16	-0.538 (±0.683)	(-1.877; 0.800)
Prop_Forest	0.16	0.229 (±0.165)	(-0.094; 0.552)	0.15	0.247 (±0.321)	(-0.383; 0.876)	0.18	0.373 (±0.517)	(-0.639; 1.386)

Table 4. Top-ranking models among 13 a priori models predicting diversity patterns for total epiphytic macrolichens, and among 5 a priori models predicting diversity patterns for *Lobarion* epiphytic macrolichens, at the tree scale in the French Northern Alps, as assessed with Akaike's information criterion corrected for small sample size (AICc). Number of estimated parameters including the intercept (k), AIC_c, AICc weight (*W*), marginal coefficient of determination for fixed effect (R^2_{GLMM}) and evidence ratio (ER), i.e. Akaike weight of the best model/Akaike weight of the second best model, are provided.

Dependent variable	Model	k	AICc	*W*	R^2_{GLMM}	ER
Total richness	Temp + Canop + Species	8	1427.6	0.538	0.362	1.55
Total cover	Temp + Canop + Species	9	2384.5	0.451	0.326	1.19
Standardized total richness	Cover + Temp + Species	8	1319.7	0.468	0.428	1.75
Lobarion richness	Canop + Diam	5	223.0	0.477	0.093	1.95
Lobarion cover	Canop + Diam	6	318.8	0.477	0.100	1.88
Standardized *Lobarion* richness	Cover + Canop + Diam	6	145.6	0.550	0.319	2.91

Table 5. Relative importance (Imp.), average coefficients (Estimate (±SE)) and confidence intervals (95% CI) for each variable predicting total and *Lobarion* epiphytic macrolichen richness and cover at the tree scale in the French Northern Alps. The 95% confidence interval of coefficients shaded excluded 0.

Parameter		Total richness			Total cover			Standardized richness		
		Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)
Cover		NA	NA	NA	NA	NA	NA	1.00	0.397 (±0.031)	(0.335; 0.459)
Lati		1.00	-0.249 (±0.073)	(-0.393; -0.105)	1.00	-0.388 (±0.110)	(-0.603; -0.173)	1.00	-0.079 (±0.048)	(-0.173; 0.014)
Temp		1.00	-0.299 (±0.077)	(-0.449; -0.149)	1.00	-0.347 (±0.111)	(-0.565; -0.129)	1.00	-0.204 (±0.050)	(-0.301; -0.107)
Canop		0.89	0.180 (±0.070)	(0.042; 0.317)	0.85	0.252 (±0.105)	(0.046; 0.459)	0.36	0.044 (±0.046)	(-0.045; 0.133)
Tree_diam		0.40	0.067 (±0.059)	(-0.048; 0.182)	0.47	0.107 (±0.079)	(-0.048; 0.263)	0.26	0.010 (±0.051)	(-0.089; 0.110)
Tree_sp	Fir - Spruce	1.00	-0.166 (±0.101)	(-0.364; 0.032)	1.00	-0.347 (±0.172)	(-0.684; -0.010)	1.00	0.084 (±0.097)	(-0.106; 0.274)
Tree_sp	Fir - Beech	1.00	-0.865 (±0.101)	(-1.063; -0.668)	1.00	-1.281 (±0.144)	(-1.563; -0.998)	1.00	-0.427 (±0.093)	(-0.608; -0.245)
Tree_sp	Fir - Decid.	1.00	-0.520 (±0.184)	(-0.881; -0.160)	1.00	-0.680 (±0.258)	(-1.185; -0.175)	1.00	-0.245 (±0.174)	(-0.585; 0.096)

Parameter		*Lobarion* richness			*Lobarion* cover			Standardized *Lobarion* richness		
		Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)	Imp.	Estimate (±SE)	(95% CI)
Cover		NA	NA	NA	NA	NA	NA	1.00	0.575 (±0.059)	(0.460; 0.691)
Lati		1.00	0.037 (±0.239)	(-0.432; 0.506)	1.00	0.163 (±0.345)	(-0.513; 0.839)	1.00	0.548 (±0.171)	(0.212; 0.883)
Temp		0.26	0.057 (±0.263)	(-0.458; 0.573)	0.26	0.081 (±0.379)	(-0.661; 0.823)	0.27	-0.022 (±0.179)	(-0.372; 0.329)
Canop		0.66	0.446 (±0.243)	(-0.030; 0.922)	0.66	0.640 (±0.353)	(-0.051; 1.331)	0.74	0.328 (±0.159)	(0.017; 0.640)
Tree_diam		1.00	0.486 (±0.161)	(0.171; 0.800)	1.00	0.693 (±0.236)	(0.230; 1.156)	1.00	0.291 (±0.109)	(0.078; 0.504)
Tree_sp	Fir - Spruce	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Fir - Beech	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Fir - Decid.	NA	NA	NA	NA	NA	NA	NA	NA	NA

Figure. 1. Study area and distribution of sampling sites among ancient and recent forests and mature and overmature stands in the French Northern Alps, France.

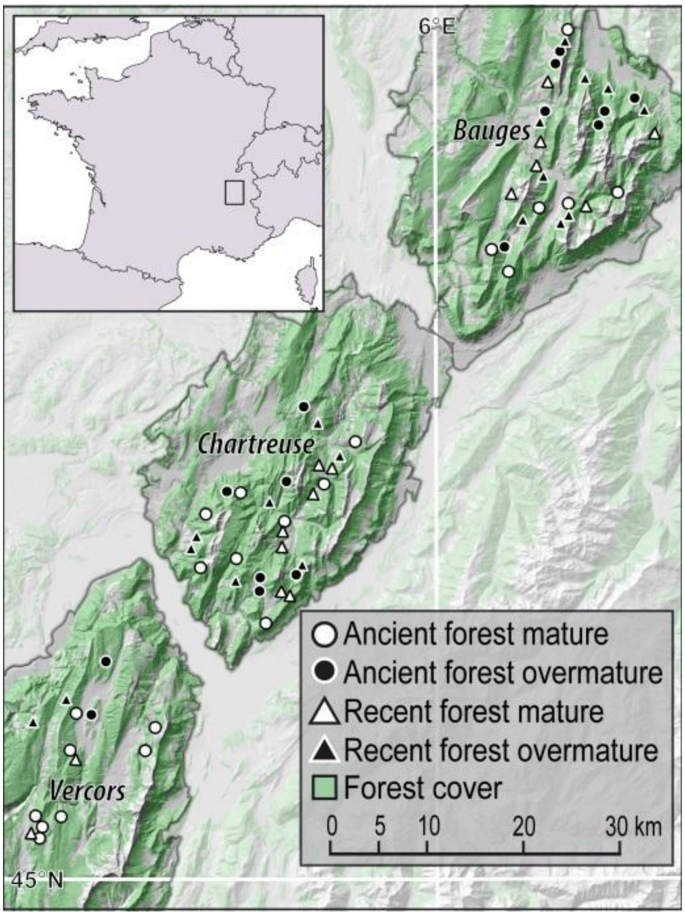

Figure 2. Canonical analysis of principal coordinates (CAP) constrained ordination of epiphytic macrolichens communities in relation to A) climate, stand and landscape variables at the stand scale (n = 70) and B) tree characteristics and environmental variables at the tree scale (n = 317).